

A PHYLOGENETIC REVIEW OF THE *POTAMOBATES* FAUNA OF
COLOMBIA (HETEROPTERA: GERRIDAE), WITH
DESCRIPTIONS OF THREE NEW SPECIES

JOHN T. POLHEMUS AND DAN A. POLHEMUS

(JTP) University of Colorado Museum, 3115 S. York St., Englewood, Colorado 80110;
(DAP) Department of Natural Sciences, Bishop Museum, P.O. Box 19000-A, Honolulu,
Hawaii 96817.

Abstract.—Three new species of *Potamobates* are described from Colombia and surrounding regions: *P. manzanoae* n. sp. from the Rio Anchicaya drainage in Valle de Cauca Province; *P. anchicaya* n. sp. from the Rio Anchicaya area and Panama; and *P. carvalhoi* n. sp. from the Rio Claro in Antioquia Province, and Venezuela. These new species are compared with other previously described taxa in the genus, and a set of phylogenetically inferred intrageneric species groupings is proposed, accompanied by a key and checklist for all known species, and a species level phylogeny. Distribution maps are provided for species occurring in Colombia, and country-level distributional data are given for all other known species.

Key Words: *Potamobates*, Gerridae, Colombia, taxonomy, phylogeny distribution, key

Due to its equatorial position and mountainous character, Colombia supports one of the richest and yet most poorly investigated aquatic Heteroptera biotas in South America. In the current report we review the region's fauna of *Potamobates* water striders, describe three new species, provide a key and checklist to all known species, and present a preliminary phylogenetic analysis of the genus at the species level. The three new taxa described herein bring the total number of documented species in the genus to 15, which we assign to four intrageneric species groups, based primarily on apomorphic characters of the male and female abdominal terminalia. Country-level distributions and complete nomenclatural citations for all described species are also provided, plus detailed distribution maps for all species occurring in Colombia.

The genus *Potamobates* was described by Champion (1898), and redescribed by Drake

and Harris (1934), Kuitert (1942) and Matsuda (1960). Members of this genus are moderately large, muscular water striders that are generally found actively skating on the midstream waters of swift, rocky streams at low to intermediate elevations. The genus is wholly Neotropical, ranging from southern Mexico to Peru, and appears to represent the Western Hemisphere ecological equivalent of the Oriental genus *Ptilomera*. Distribution data and keys to species were previously published by Drake and Harris (1934) and Kuitert (1942), but these authors did not have access to all of the known species, and their omissions plus the three new species described below have necessitated the development of the revised key presented herein.

All measurements in the descriptions below are given in millimeters. CL numbers following localities in the material examined sections refer to a data coding system

used by the authors to cross reference specimens, ecological field notes, and habitat photographs.

***Potamobates carvalhoi*, NEW SPECIES**

Figs. 1–6, 19

Diagnosis.—*Potamobates carvalhoi* occupies a phylogenetic position immediately basal to the insular South American *P. williamsi* group (see Figs. 30, 31), but is set aside in its own monotypic intrageneric grouping because of the unusual and diagnostic character of the abdominal terminalia in both males and females (see subsequent group analysis). The completely hidden female tergite VIII is unique within the genus.

Description (all measurements in millimeters).—*Apterous male*: Ground color blackish, faintly shining, covered with very short dark pubescence; head except vertex along eyes and longitudinal oval black spot ahead of eyes, median longitudinal wedge on pronotum, figures on mesonotum if present (Fig. 2), propleura, mesopleura, metacephalae, coxae, fore trochanters, dorsum of fore femur except distally, pygophore and venter brownish yellow to leucine. Anterolateral angles of pronotum, longitudinal stripe on lateral margins and posterolateral angles of mesonotum, lateral margins of abdominal tergites, and coxal cavities dorsally covered with short bright golden pubescence. Legs black to brown, middle and hind femora lighter beneath, antennae black. Legs set with short inconspicuous black spines.

Length of head (1.22) more than four times narrowest interocular space (0.28); width of eye 0.72; eyes extending posteriorly about $\frac{1}{2}$ length of propleura. Rostrum short, barely reaching onto mesosternum. Pronotum short (1.05), width (1.89) about equal to head across eyes. Mesonotum long (2.33), widest across mesocoxae (2.89). Metanotum short (0.83), widest across metacoxae (2.39). Abdomen excluding genital segments relatively short (2.33), genital segments long (2.05). Tergites III–V about

of equal length (0.17–0.22), tergites II and VI longer (0.28), tergite VII longest (0.67); VIII long (1.44), large, slightly modified, ventrally asymmetrical (Figs. 2, 5, 6); proctiger modified, with long projection on left side, terminating in a “bird-head” shape; male terminalia as shown in Figs. 5, 6. Connexiva angulate caudally, not produced; raised along entire length.

Antennae long, slender, segments I and IV slightly stouter than II and III; length of segments I–IV: 1.83; 0.61; 0.67; 1.00. Anterior femur stout, tapering distally; anterior tibia slightly flattened, not dilated. Measurements of legs as follows: Femur, tibia, tarsal 1, tarsal 2 of fore leg, 2.55: 2.61: 0.14: 0.50; of middle leg, 9.43: 6.94: 3.33: 0.94; of hind leg, 9.82: 6.60: 0.44: 0.28.

Length, mean 9.68 (N = 6, min. 9.50, max. 9.86).

Width, mean 2.93 (N = 6, min. 2.84, max. 3.04).

Apterous female: Body more robust than male (Fig. 1), otherwise similar in general size, coloration, and other features except abdominal terminalia very differently formed. Connexiva produced posteriorly into long slender digitate lobes, usually convergent (Fig. 3). Abdominal ventrite VIII produced symmetrically, lateral lobes large, folded over tergite VIII which is hidden (Figs. 3, 4).

Length, mean 8.84 (N = 10, min. 8.61, max. 9.14).

Width, mean 3.13 (N = 10, min. 3.02, max. 3.29).

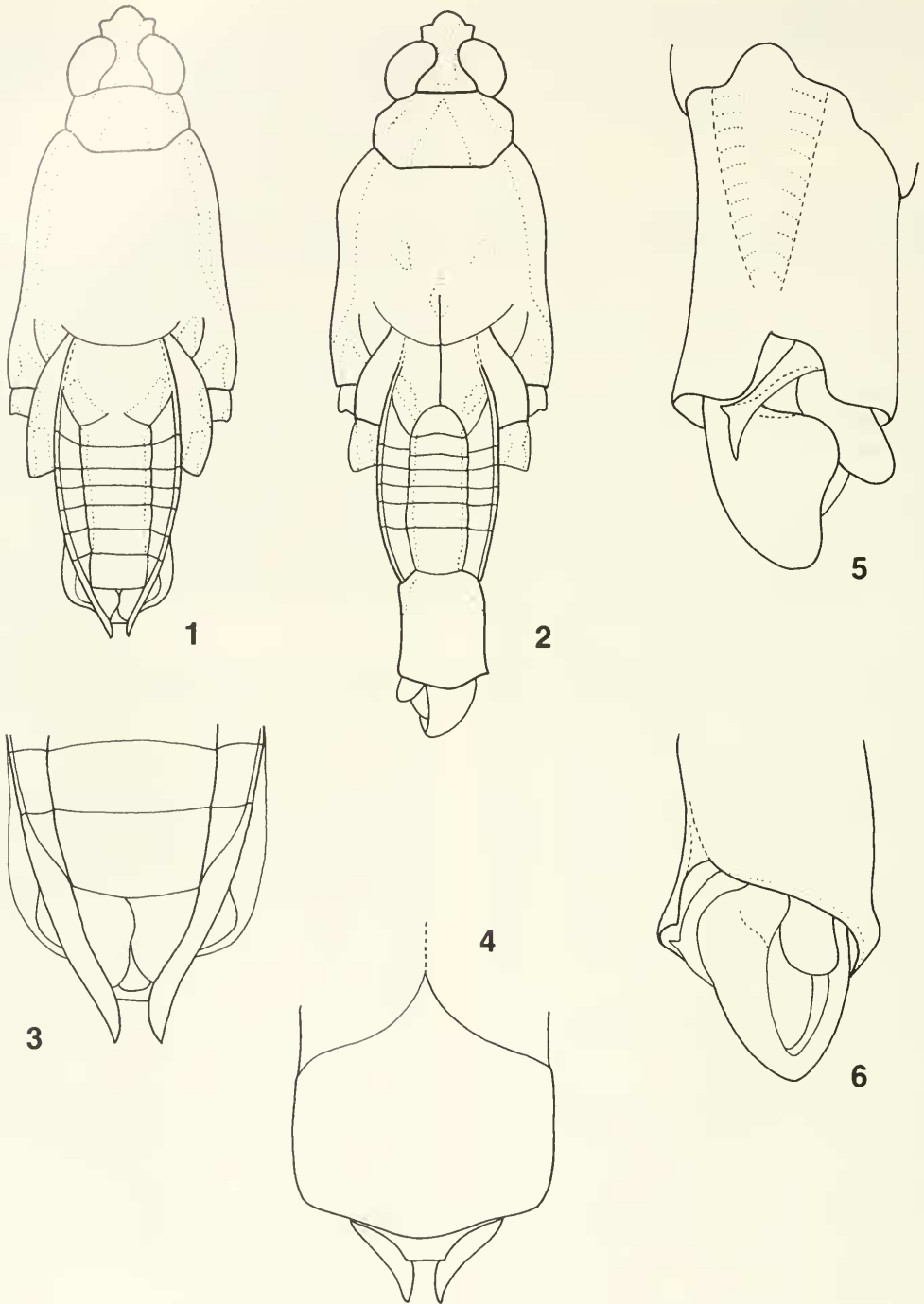
Macropterous male: Similar to apterous form in most respects, except pronotum long, with posterior lobe raised and broadly margined with brownish yellow, humeri prominent. Wings light brown, reaching beyond tip of abdomen, veins blackish brown, without pubescence, with five closed cells.

Length, 11.28 (N = 1).

Width, 3.02 (N = 1).

Macropterous female: Unknown.

Etymology.—The name *carvalhoi* honors José Candido de Melo Carvalho for his many



Figs. 1-6. *Potamobates carvalhoi* n. sp. 1, Female, dorsal habitus (legs omitted). 2, Male, dorsal habitus (legs omitted). 3, 4, Female terminal abdomen. 3, Dorsal view. 4, Ventral view. 5, 6, Male terminal abdomen, showing distal part of segment VII, all of VIII, IX & X partially hidden within VIII. 5, Lateral view. 6, Oblique ventral view.

splendid contributions to our knowledge of Heteroptera.

Ecological notes.—*P. carvalhoi* was taken in midstream, skating in areas of slow, smoothly flowing current.

Material examined.—*Holotype*, apterous male and allotype, apterous female (USNM), COLOMBIA: Antioquia Prov., Rio Claro, 13 km W. of Dorodal, water temp. 25 °C, 250 m, CL 2405, 21.vii.1989, J. T. & D. A. Polhemus. *Paratypes* as follows (all apterous unless noted): COLOMBIA: Antioquia Prov.: 4 males, 5 females, 1 macropterous female, same data as holotype (JTTC, USNM); 2 males, 5 females, Quebrada La Negra, small tributary to Rio Claro, 13 km W. of Dorodal, 250 m, CL 2406, 21.vii.1989, J. T. & D. A. Polhemus (JTTC). VENEZUELA: Barinas Prov.: 2 males, 4 females, Barinitas, Dec. '42, P. Anduzee (det. C. J. Drake as *P. unidentatus*) (JTTC, USNM).

***Potamobates anchicaya*, NEW SPECIES**

Figs. 7–13, 21

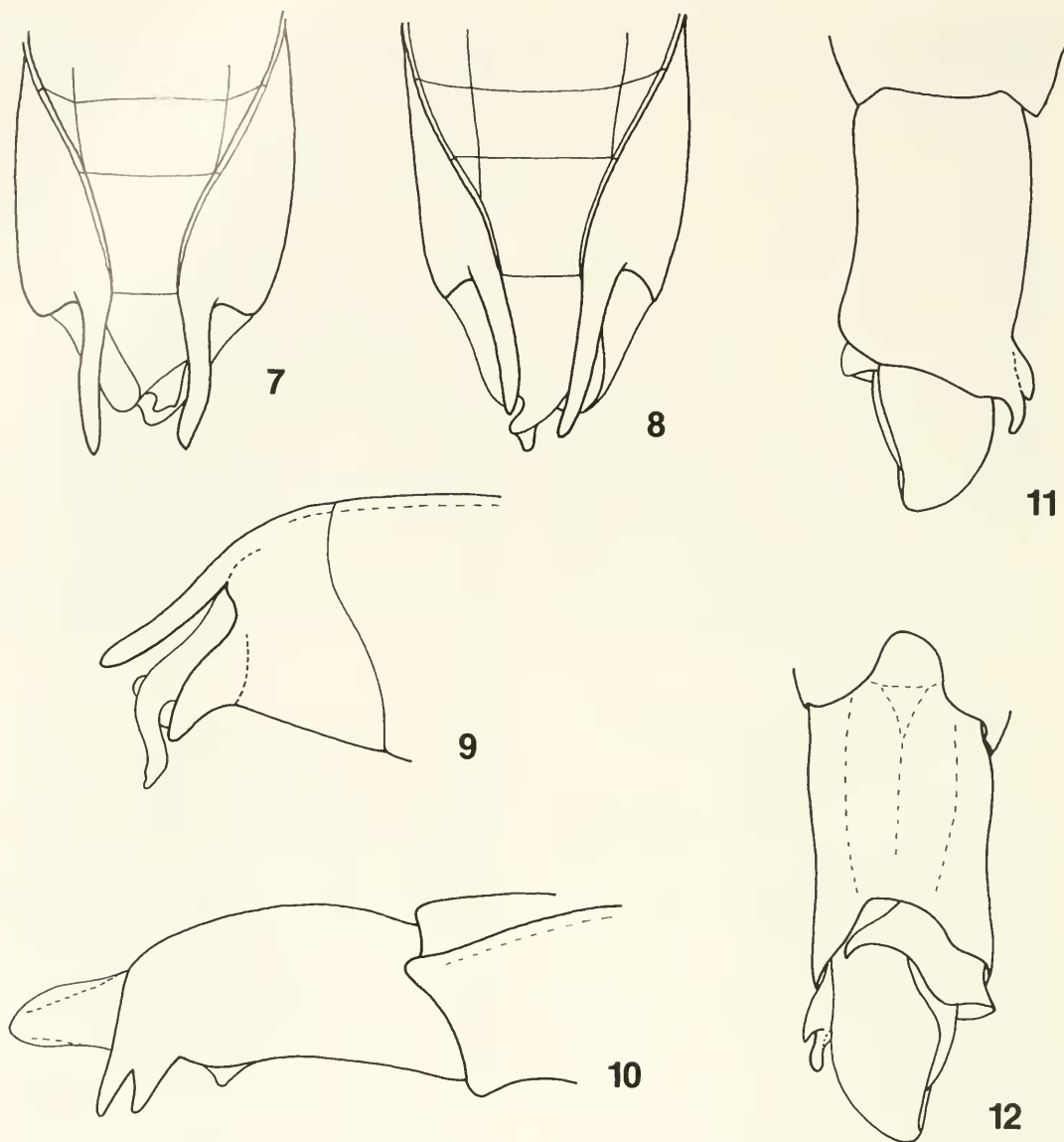
Diagnosis.—*Potamobates anchicaya* is most closely related to *P. tridentatus* Esaki, but compared to the latter *anchicaya* may be separated by the narrower silvery pubescent stripe laterally on the mesonotum; the less pronounced incision between the “teeth” on the lobe of male abdominal segment VIII, and in having this lobe of different shape (Fig. 10; compare with Esaki 1926, Fig. 1e); by the emarginate ventral incision of male abdominal segment VIII being narrower and shallower, and the laterally directed process of the proctiger larger, longer and of different shape (Fig. 12; compare with Esaki 1926, Fig. 1d); and by female ventrite VIII extending posteriorly about the length of ventrite VI (vs. about ½ the length of ventrite VI in *tridentatus*), unless strongly bent ventrad (vs. never strongly bent ventrad), and with the lateral lobes less asymmetrical, having both right and left lobes developed (vs. left lobe developed), with one or both sometimes wrapped over

tergite VIII basally (vs. left lobe wrapped over or at least alongside).

Description (all measurements in millimeters).—*Apterous male*: Ground color blackish, faintly shining, covered with very short dark pubescence; head except vertex along eyes and often longitudinal oval black spot ahead of eyes, median longitudinal wedge on pronotum, figures on mesonotum (Fig. 13), propleura, mesopleura, metacephalae, coxae, fore trochanters, dorsum of fore femur except distally, pygophore and venter brownish yellow to leucine. Anterolateral angles of pronotum, longitudinal stripe on lateral margins and posterolateral angles of mesonotum, lateral margins of abdominal tergites, and coxal cavities dorsally covered with short bright golden pubescence. Legs black to brown, middle and hind femora lighter beneath basally, antennae black. Legs set with short inconspicuous black spines.

Length of head (1.05) about four times narrowest interocular space (0.28); width of eye 0.58; eyes extending posteriorly about ½ length of propleura. Rostrum short, barely reaching onto mesosternum. Pronotum short (0.83), width (1.39) about equal to head across eyes. Mesonotum long (2.44), widest across mesocoxae (2.55). Metanotum short (0.78), widest across metacoxae (2.05). Abdomen excluding genital segments relatively short (2.22), genital segments long (2.00). Tergites II–VI about of equal length (0.22–0.28), tergite VII about twice as long (0.55); VIII long (1.39), large, highly modified, with a lobe on left side bearing two large “teeth” (Fig. 10); proctiger highly modified, with long projection on left side (Fig. 12); male terminalia as shown in Figs. 10–12. Connexiva angulate caudally, not produced; raised along entire length.

Antennae long, slender, segments I and IV slightly stouter than II and III; length of segments I–IV: 1.55; 0.57; 0.50; 0.89. Anterior femur stout, tapering distally; anterior tibia slightly flattened, not dilated. Measurements of legs as follows: Femur, tibia,



Figs. 7-12. *Potamobates anchicaya* n. sp. 7-9, Female terminal abdomen. 7, Dorsal view, without caudal projection. 8, Dorsal view. 9, Lateral view. 10-12, Male terminal abdomen. 10, Lateral view. 11, Dorsal view. 12, Oblique ventral view.

tarsal 1, tarsal 2 of fore leg, 2.33: 2.11: 0.14: 0.44; of middle leg, 8.55: 5.77: 2.39: 0.61; of hind leg, 9.26: 4.83: 0.36: 0.22.

Length, mean 9.36 (N = 10, min. 9.24, max. 9.59).

Width, mean 2.50 (N = 10, min. 2.31, max. 2.75).

Apterous female: Body more robust than male, otherwise similar in general size, coloration, and other features except dark markings on head usually more extensive, and abdominal terminalia very differently formed. Connexiva produced posteriorly into long slender digitate lobes, usually al-

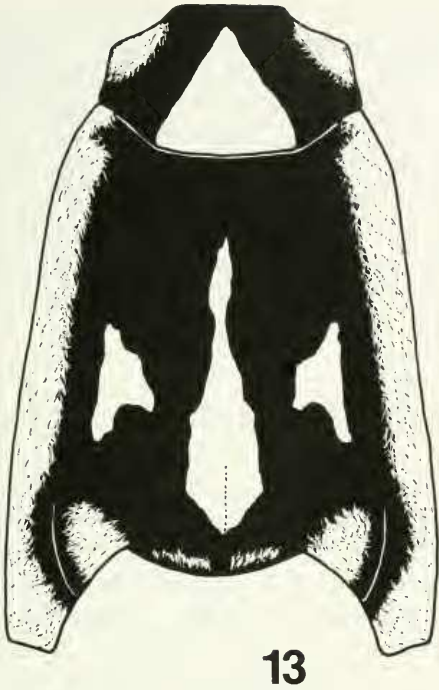


Fig. 13. *Potamobates anchicaya* n. sp. Thorax, dorsal view.

most parallel distally, sometimes divergent (Figs. 7, 8). Abdominal ventrite VIII produced asymmetrically, embracing or paralleling tergite VIII which may be either truncate (Fig. 7) or produced into a sinuate spine (Figs. 8, 9).

Length, mean 8.59 (N = 10, min. 8.08, max. 9.24).

Width, mean 2.70 (N = 10, min. 2.58, max. 2.84).

Macropterous male: Similar to apterous form in most respects, except pronotum long, with posterior lobe raised and broadly margined with brownish yellow, humeri prominent. Wings light brown, reaching beyond tip of abdomen, veins blackish brown, without pubescence, with five closed cells; wings often mutilated, presumably to facilitate mating, sometimes without even basal stub remaining.

Length, mean 10.42 (N = 6, min. 10.12, max. 10.57; de-alated specimens not measured).

Width, mean 2.56 (N = 6, min. 2.49, max. 2.66).

Macropterous female: Similar to macropterous male in most respects, except slightly broader, and wings reaching far beyond tip of abdomen.

Length, mean 10.46 (N = 5, min. 10.39, max. 10.66; de-alated specimens not measured).

Width, mean 2.79 (N = 5, min. 2.66, max. 2.84).

Etymology.—The name *anchicaya*, a noun in apposition, refers to the type locality, the valley of the Rio Anchicaya.

Ecological notes.—*Potamobates anchicaya* was taken in midstream on swift, smoothly flowing reaches above riffles, in company with *Metrobates fugientis* Drake and Harris. *Potamobates horvathi* was also present at the type locality, but was found on the slower waters of pools both above and below riffles, and not in the midstream areas favored by *P. anchicaya*.

Remarks.—*Potamobates* species are highly variable in the development and shape of the bizarre modifications of the abdominal terminalia in both males and females, which led previous workers to overlook or misidentify specimens of *P. anchicaya* in their collections. *Potamobates anchicaya* specimens from Panama, for example, were identified as *P. tridentatus* Esaki by both Drake (in Drake Collection, USNM) and Hungerford (1937b). For many years specimens of *anchicaya* from the Canal Zone of Panama in the Polhemus collection have been marked as “not *tridentatus*,” but a satisfactory delineation was possible only with good series of both species available from a number of localities.

Material examined.—*Holotype*, apterous male and allotype, apterous female (USNM), COLOMBIA: Valle de Cauca Prov., Rio Tatabro, 7 km E. of Sabaletas, water temp. 24 °C, CL 2436, 30.vii.1989, J. T. & D. A. Polhemus. *Paratypes* as follows (all in JTPC, all apterous unless noted): COLOMBIA: Valle de Cauca Prov.: 4 males, 3 macrop-

terous males, 8 females, 3 macropterous females, 3 nymphs, same data as holotype; 14 males, 1 female, swift rocky tributary to Rio Anchicaya, east of CL 2436, 100 m, water temp. 24 °C, CL 2435, 30.vii.1989, J. T. & D. A. Polhemus; 11 males, 11 females, 2 nymphs, small forest stream near Bajo Calima research station, NE of Buenaventura, 40 m, water temp. 25 °C, CL 2437, 30.vii.1989, J. T. & D. A. Polhemus; 1 male, 2 females, Bajo Calima, 3.iii.1987, M. R. Manzano (NNC); 4 males, 2 females, Rio Tatabro, 7 km E. of Sabaletas, 1.ii.1987, #87004, Gonzáles (NNC; JTPC); 3 males, 3 females, Gorgona, Quebrada Acueducto, 30.xii.1989, M. Baena (NNC); 1 male, 1 macropterous female, Rio San Cipriano, 40 m, 7.viii.1989, M. R. Manzano (UVCC). PANAMA: Panamá Prov. (all collected by JTP unless noted): 1 male, 1 macropterous male, La Cascada, small stream and waterfall on Madden Highway, about 4 km S. of Maria Eugenia, trib. of Rio Pedro Miguel, ~100 m, water temp. 24 °C, CL 2771, 31.xiii.1992, J. T. Polhemus & A. R. Gillogly; 5 males, 1 macropterous male, 3 females, 2 macropterous females, 1 nymph, Rio Juan Grande, off Pipeline Road, nr. Gamboa, km 2, ~30 m, CL 2784, 5.i.1993; 4 males, 1 female, 1 nymph, Rio Agua Salud, off Pipeline Road, km 17, ~5 m, CL 2785, 5.i.1993; 3 males, 3 females, 2 nymphs, unnamed stream off Pipeline Road, km 13.8, ~5 m, CL 2786, 5.i.1993; 1 female, unnamed stream off Pipeline Road, km 15, ~5 m, CL 2789, 6.i.1993; 7 males, 6 females, small unnamed stream off Pipeline Road, km 10.6, ~5 m, CL 2790, 6.i.1993; 1 female, small unnamed stream off Radar Site road S. of Gamboa, ~50 m, CL 2795, 7.i.1993; 1 male, 2 macropterous males, 2 macropterous females, stream crossing road between Gamboa Rd. and Cascada on Madden Hwy., ~50 m, CL 2796, 7.i.1993; 1 male, Rio Indio, Altos del Cerro Azul, E. of Panama City, 560 m, CL 2799, 8.i.1993; 2 females, stream on main road past Altos del Cerro Azul, 26.5 km from Pan Am Hwy. nr. Villa Linda, E. of

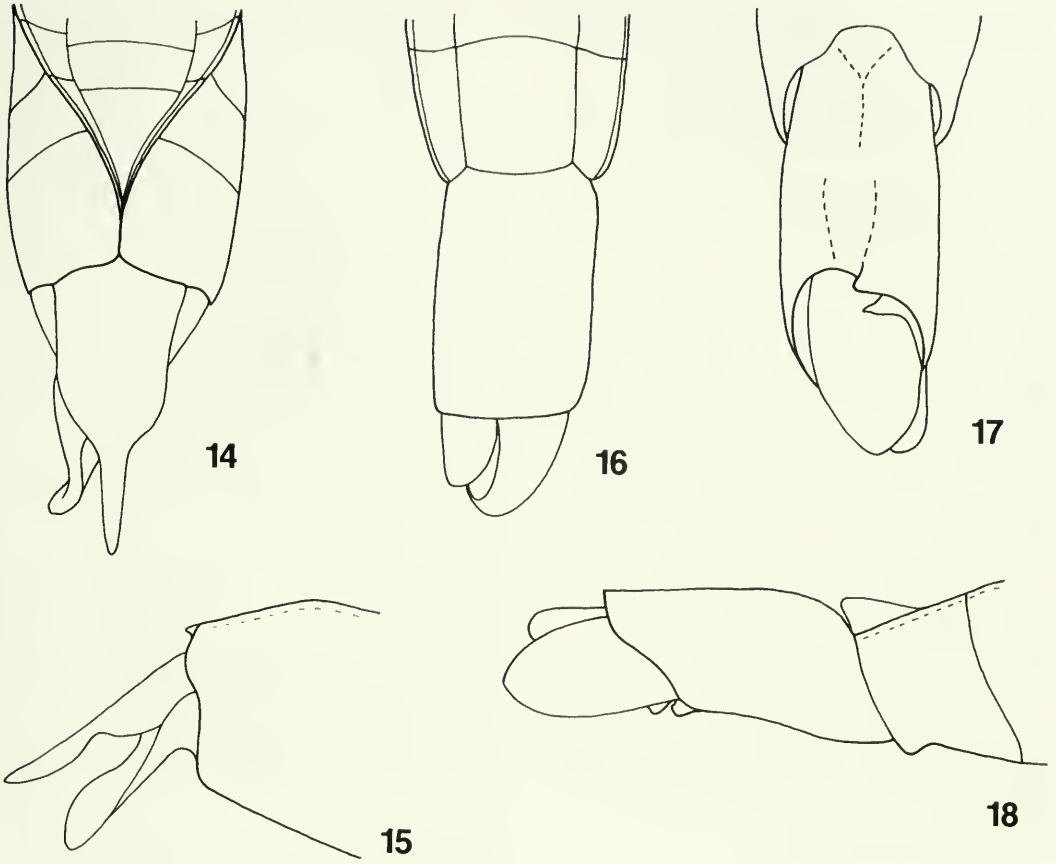
Panama City, ~900 m, CL 2800, 8.i.1993; 1 apterous male, N. of Portobello, CL 1296, 2.i.1970; 1 apterous female, Canal Zone, 10.ii.1939, C. J. Drake; 1 apterous male, 1 apterous female, Pearl Islands, San Jose, 30.vii.1944, J. P. E. Morrison. San Blas Prov.: 7 males, 1 macropterous male, 2 females, 3 macropterous females, Rio Nusagandi, west of Nusagandi, ~200 m, water temp. 24.5 °C, CL 2772, 1.i.1993, J. T. Polhemus & A. R. Gillogly.

Potamobates manzanoae, NEW SPECIES

Figs. 14–18, 20

Diagnosis.—*Potamobates manzanoae* is a sister species to *P. unidentatus* Champion (see Figs. 30, 31), but compared to the latter *manzanoae* may be separated by the shorter yellowish stripe medially on the mesonotum, which does not extend anteriorly much beyond the middle (vs. reaching to pronotum in *unidentatus*); the laterally directed process of proctiger, which is larger, longer and of different shape (process in *unidentatus* small, usually hidden); and the unique, bizarre female abdominal terminalia, not resembling those of any other species (Figs. 14, 15).

Description (all measurements in millimeters).—*Apterous male*: Ground color blackish, faintly shining, covered with very short dark pubescence; head except vertex along eyes and longitudinal oval black spot ahead of eyes, median longitudinal wedge on pronotum, figures on mesonotum (similar to *P. anchicaya* but somewhat smaller; see Fig. 13), propleura, mesopleura, metacephalae, coxae, fore trochanters, dorsum of fore femur except distally, and venter brownish yellow to leucine. Anterolateral angles of pronotum, longitudinal stripe on lateral margins and posterolateral angles of mesonotum, lateral margins of abdominal tergites, and coxal cavities dorsally covered with short bright golden pubescence. Legs black to brown, middle and hind femora lighter beneath basally, antennae black. Legs set with short inconspicuous black spines.



Figs. 14–18. *Potamobates manzanoae* n. sp. 14, 15, Female terminal abdomen. 14, Dorsal view. 15, Lateral view. 16–18, Male terminal abdomen. 16, Dorsal view. 17, Ventral view. 18, Lateral view.

Length of head (1.17) about four times narrowest interocular space (0.28); width of eye 0.61; eyes extending posteriorly about $\frac{1}{2}$ length of propleura. Rostrum short, barely reaching onto mesosternum. Pronotum short (0.83), width (1.44) about equal to head across eyes. Mesonotum long (2.72), widest across mesocoxae (2.66). Metanotum short (0.88), widest across metacoxae (2.33). Abdomen excluding genital segments relatively short (2.55), genital segments long (2.00). Tergites II–V about of equal length (0.17–0.22), tergite VI longer (0.33), tergite VII longest (0.67); VIII long (1.33), large, modified, asymmetrical beneath (Fig. 17); procotiger highly modified, with long projection on left side (Fig. 17); male terminalia as shown in Figs. 16–18. Connexiva angulate

caudally, not produced; slightly raised along entire length.

Antennae long, slender, segments I and IV slightly stouter than II and III; length of segments I–IV: 1.83; 0.67; 0.67; 1.00. Anterior femur stout, tapering distally; anterior tibia slightly flattened, not dilated. Measurements of legs as follows: Femur, tibia, tarsal 1, tarsal 2 of fore leg, 2.77; 2.60; 0.11; 0.44; of middle leg, 9.05; 6.22; 2.77; 0.72; of hind leg, 9.54; 5.38; 0.50; 0.28.

Length, mean 9.72 (N = 2, min. 9.41, max. 10.04).

Width, mean 2.58 (N = 2, min. 2.49, max. 2.66).

Apterous female: Body more robust than male, otherwise similar in general size, coloration, and other features except dark

markings on head usually less extensive, and abdominal terminalia very differently formed. Connexiva truncate, not produced (Fig. 14). Abdominal ventrite VIII strongly produced posteriorly, long, asymmetrical, twisted, spatulate; tergite VIII long, produced, acuminate distally (Figs. 14, 15).

Length, 9.24 (N = 1).

Width, mean 2.84 (N = 1).

Macropterous male: Similar to apterous form in most respects, except pronotum long, with posterior lobe raised and broadly margined with yellowish, humeri prominent. Wings light brown, reaching beyond tip of abdomen, veins blackish brown, without pubescence, with four closed cells, distal cell open.

Length, mean 10.39 (N = 2, min. 10.30, max. 10.48).

Width, mean 2.53 (N = 2, min. 2.49, max. 2.58).

Macropterous female: Similar to macropterous male in most respects, except slightly broader, and wings reaching far beyond tip of abdomen.

Length, 10.39 (N = 1).

Width, 2.75 (N = 1).

Etymology.—The name *manzanoae* honors Maria Rosario Manzano for her contributions to our knowledge of the aquatic Heteroptera of Colombia.

Ecological notes.—*P. manzanoae* was taken in midstream in areas of swift, smooth current.

Material examined.—*Holotype*, apterous male and allotype, apterous female (USNM), COLOMBIA: Valle de Cauca Prov., swift rocky tributary to Rio Anchicaya, water temp. 24 °C, CL 2435, 30.vii.1989, J. T. & D. A. Polhemus. *Paratypes* as follows (all in JTPC, all apterous unless noted): COLOMBIA: Valle de Cauca Prov.: 1 male, 1 macropterous male, 1 female, 1 macropterous female, same data as holotype; 1 male, 1 female, Rio Danubio, 35 km W. of Quereamal, CL 2432, 30.vii.1989, J. T. & D. A. Polhemus.

Potamobates tridentatus Esaki

Fig. 19

The range of *P. tridentatus* extends from northern Costa Rica southward to Chiriqui Province in northern Panama. Repeated collections southward have not revealed any intervening populations between Chiriqui Province and the region of the Panama Canal Zone, where *P. anchicaya* is common. Esaki (1926) provided splendid figures of the abdominal terminalia of both males and females that illustrate the differences between these two species (see discussion under *P. anchicaya*).

Wheelwright and Wilkinson (1985) studied the ecology of *P. tridentatus* in the Osa Peninsula of Costa Rica.

Material examined.—(all in JTPC, all apterous unless noted). COSTA RICA: Guanacaste Prov.: 1 male, 12.vii.1957, D. R. Leach. Puntarenas Prov.: 1 male, 2 females, Cañas, Rio Lagarto, 9.xi.1981, E. Berrera & H. Brailovsky; 2 males, 1 macropterous male, 2 females, 1 macropterous female, river 24 km N of Esparta, CL 1264, 24.xii.1969, J. T. Polhemus. PANAMA: Chiriquí Prov.: 5 males, 1 female, Balneario, river 3.8 km N of David, CL 2819, 13.i.1993, J. T. Polhemus & A. R. Gilgoly; 1 female, small stream ~110 km S of David, CL 1289, 31.xii.1969, J. T. Polhemus.

Potamobates horvathi Esaki

Fig. 20

This is the commonest and most widespread species in the genus, with a range from southern Mexico to Colombia. It occurs in both the Atlantic and Pacific drainages, usually at low elevations.

Matsuda (1961) studied the relative growth of all nymphal instars and adults of this species in a Panamanian population.

Material examined.—(all in JTPC, all apterous unless noted). BELIZE: 1 male, Rio Grande, Nov. 1931; 2 females, Punta Gorda, 1932. COLOMBIA: Valle de Cauca Prov.: 4 males, 4 females, Rio Tatabro, 7 km E. of Sabaletas, water temp. 24 °C, CL



Fig. 19. Distributions of *Potamobates* species. Solid triangles: *P. tridentatus* Esaki. Open triangle: *P. carvalhoi* n. sp.

2436, 30.vii.1989, J. T. & D. A. Polhemus; 3 males, 1 macropterous male, 1 female, 2 macropterous females, Rio San Cipriano, 40 m, 7.viii.1989, M. T. Manzano (UVCC). COSTA RICA: Guanacaste Prov.: 4 males, 2 macropterous males, 4 females, 3 macropterous females, 1 nymph, Rio Sanzapote, 6 km N of La Cruz, nr. Nicaragua border, CL 1307, 8.i.1970, J. T. Polhemus. Puntarenas Prov.: 6 males, 2 macropterous males, 4 females, 1 macropterous female, 1 nymph, river 24 km N of Esparta, CL 1264, 24.xii.1969, J. T. Polhemus. GUATEMALA: 1 male, Esquintla; 2 males, 1 female, Los Amates; 2 males, 7 females, 1 macropterous female, small river, Azucho, 24 km S of Esquintla, CL 1252, 20.xii.1969, J. T. Polhemus; 5 males, 2 macropterous males,

1 female, Stain Creek, 11 km N of Zacapa, CL 1316, 11.i.1970, J. T. Polhemus; 5 males, 1 nymph, stream, E of Quirigua, CL 1317, 11.i.1970, J. T. Polhemus. HONDURAS: 1 male, Lancetilla, 22.iii.1936, John Deal. NICARAGUA: 15 males, 4 females, small stream, 13 km N of Esteli, CL 1262, 23.xii.1969, J. T. Polhemus. PANAMA: Bocas del Toro Prov.: 2 males, 5 females, deep stream on road to oil tanks, S. of Chiriquí Grande, sea level, CL 2829, 14.i.1993, J. T. Polhemus & A. R. Gillogly; 1 male, 1 female, vegetated stream, 5.1 km S. Punta Peña, ~50 m, CL 2830, 14.i.1993, J. T. Polhemus & A. R. Gillogly. Chiriquí Prov.: 1 macropterous female, Balneario, river 3.8 km N of David, CL 2819, 13.i.1993, J. T. Polhemus & A. R. Gillogly; Colon Prov.: 2



Fig. 20. Distributions of *Potamobates* species. Solid triangles: *P. horvathi* Esaki. Open triangle: *P. manzanaoae* n. sp.

males, 2 females, 2 km N of Maria Chiquita, 27.ii.1993, A. R. Gillogly; 2 males, 4 females, 3 nymphs, N of Portobello, sea level, CL 1296, 2.i.1970, J. T. Polhemus. Herrera Prov.: 1 male, 1 macropterous male, 3 females, Rio Paritas, 2.8 km S of Ocu, CL 2802, 9.i.1993, J. T. Polhemus & A. R. Gillogly; Panamá Prov.: 3 males, 1 macropterous male, 3 females, 2 macropterous females, Rio Cabra, ~3 km N of jct. to Altos Cerro Azul, ~20 m, CL 2797, 7.i.1993, J. T. Polhemus; 7 males, 16 females, 5 km N of San Carlos, CL 1300, 4.i.1970, J. T. Polhemus; 2 males, Panama City, ii.1939, C. J. Drake; 1 macropterous male, Canal Zone, 10.ii.1939, C. J. Drake; 9 males, 7 females, 3 nymphs, E of Panama City, CL 1295, 2.i.1970, J. T. Polhemus.

Potamobates unidentatus Champion
Fig. 22

This species is common and widespread throughout Costa Rica and Panama, occurring in both the Pacific and Atlantic watersheds, in contrast to *P. tridentatus* which has so far been found only in Pacific drainages. We did not collect this species during our surveys in Colombia, and to our knowledge it has been reported from the country only once, at Mamatoco, Magdalena Province (Esaki 1926).

Matsuda (1961) studied the relative growth of all nymphal instars and adults of this species in a Costa Rican population.

Material examined.—(all in JTPC, all apterous unless noted). COSTA RICA: Car-



Fig. 21. Distributions of *Potamobates* species. Solid triangles: *P. vivatus* Drake & Roze. Open triangle: *P. anchicaya* n. sp.

tago Prov.: 1 male, 1 female, km 20, Turrialba—Siquirres Rd., 22.ii.1982, E. Berrera. Heredia Prov.: 19 males, 1 macropterous male, 18 females, 1 macropterous female, Ojo de Agua, nr. San Antonio, CL 1269, 25.xii.1969, J. T. Polhemus. Limon Prov.: 1 male, 2 females, Rio Santa Clara, Guapiles, 26.iv.1984, E. Berrera. Puntarenas Prov.: 1 male, 2 macropterous males, 3 females, 3 macropterous females, 1 nymph, Rio Java, nr. San Vito de Java, CL 1283, 29.xii.1969, J. T. Polhemus. PANAMA: Bocas del Toro Prov.: 2 males, 4 females, stream 6.6 km N. of Continental Divide on rd. to Chiriqui Grande, ~600 m, CL 2824, 13.i.1993, J. T. Polhemus & A. R. Gillogly; 6 males, 4 females, tributaries to Rio Hornitos, Reserva la Fortuna, 1400 m, CL 2825,

14.i.1993, J. T. Polhemus & A. R. Gillogly. Coclé Prov.: 1 male, 2 females, stream in forest below El Valle, CL 1299, 3.i.1970, J. T. Polhemus. Panamá Prov.: 2 males, 1 female, 1 macropterous female, Rio Indio, Altos Cerro Azul, 558 m, CL 2799, 8.i.1993, J. T. Polhemus; 1 male, small stream nr. Villa Linda, W. of Altos Cerro Azul, 26 km from Pan Am Hwy, ~900 m, CL 2800, 8.i.1993, J. T. Polhemus. San Blas Prov.: 1 male, 1 female, Rio Nusagandi, W. of Nusagandi, ~200 m, CL 2772, 1.i.1993, J. T. Polhemus & A. R. Gillogly; 4 males, 9 females, small stream nr. Nusagandi, ~500 m, CL 2774, 2.i.1993, J. T. Polhemus; 2 males, 4 females, waterfall ~5 km E. of Nusagandi, ~450 m, CL 2775, 2.i.1993, J. T. Polhemus & A. R. Gillogly.



Fig. 22. Distribution of *Potamobates unidentatus* Champion.

Potamobates vivatus Drake and Roze

Fig. 21

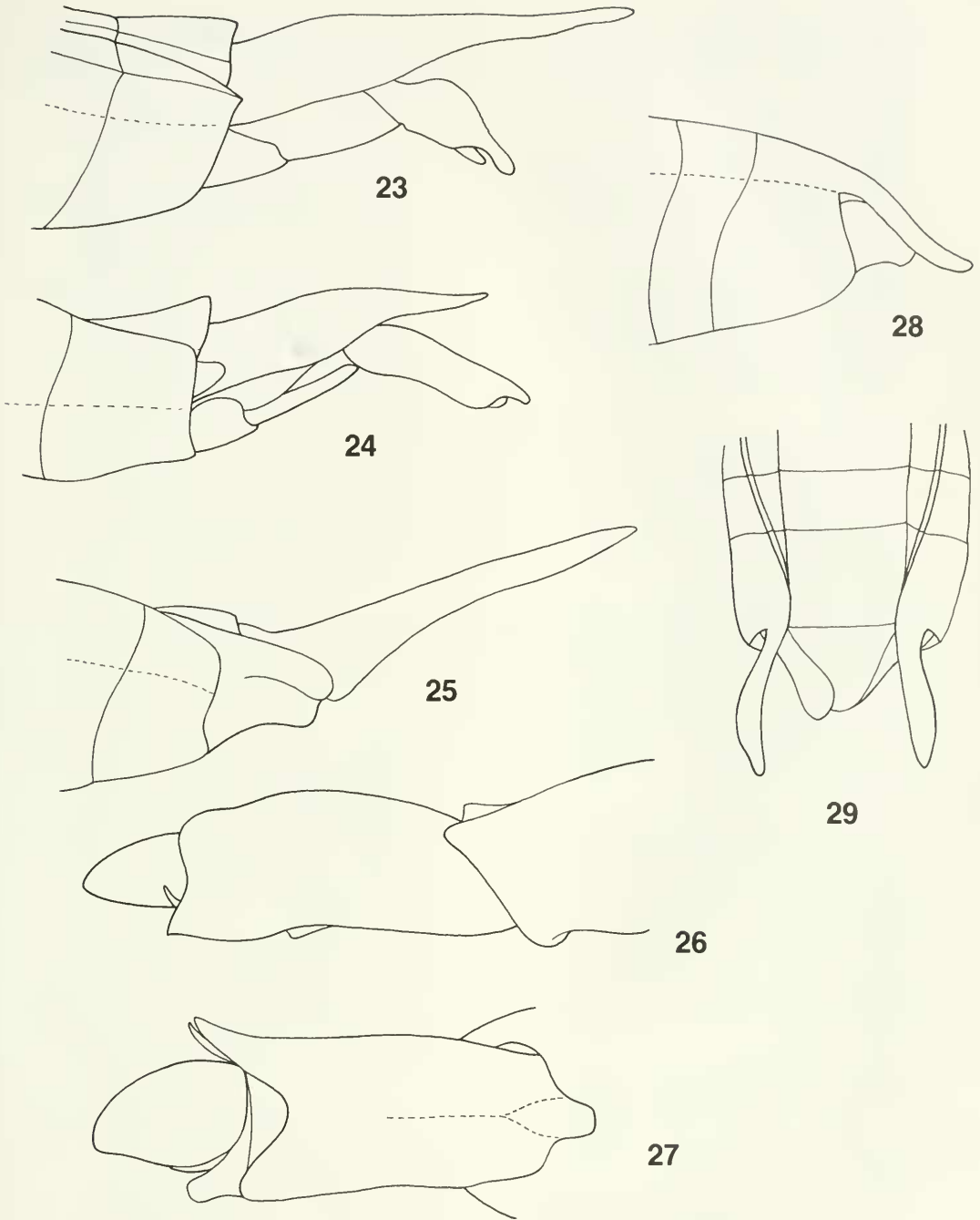
This species was originally described from two localities in the coastal ranges of northern Venezuela. We did not collect this species in Colombia, and to our knowledge it has been taken in this country at only a single locality, the Serrania de la Macarena in Meta Province, an isolated sandstone massif lying to the east of the main Andean uplift (Fig. 21).

Material examined.—(all in JTPC, all apterous unless noted). COLOMBIA: Meta Prov.: 7 males, 1 macropterous male, 5 females, 4 nymphs, Rio Santo Domingo, Serrania de la Macarena, 24.i.1989, C. Murillo (JTPC, UVCC). VENEZUELA: Distrito Federal: 1 male paratype, Cerro el Avila, 16.viii.1952, J. A. Roze; Carabobo Prov.:

1 female paratype, Belén, 27.vi.1953, J. A. Roze.

KEY TO THE SPECIES OF *POTAMOBATES*

Species keys were last published for the genus *Potamobates* by Drake and Harris (1934) and Kuitert (1942). The former included only six, and the latter only ten, of the fifteen presently known species, therefore a new key is provided below, including all described taxa. A fully illustrated key, though desirable, was beyond the scope of this paper, whose primary focus is the fauna of Colombia; the present key thus makes reference to previously published figures, with new illustrations being provided only for those species in which one or both sexes have never before been figured.



Figs. 23–29. *Potamobates* spp., abdominal terminalia. 23, *P. osborni* Drake & Harris, female, lateral view. 24, *P. bidentatus* Champion, female, lateral view. 25–27, *P. vivatus* Drake & Roze; 25, female, lateral view; 26, male, lateral view; 27, male, ventral view. 28, 29, *P. williamsi* Hungerford, female; 28, lateral view; 29, postero-dorsal view.

- 1. Pronotum medially with a roughly parallel sided linear longitudinal yellow stripe. Male abdominal segment VIII modified, segments IX, X rotated a maximum of 45° 2
- Pronotum medially with a roughly triangular or wedge shaped yellow mark. Male abdominal segment VIII modified (except *thomasi*), segments IX, X rotated variably in each species, from about 10° to about 90° 5
- 2(1). Male abdominal segment VIII not modified; segments IX, X not rotated. Female with short sharp connexival spines, and a pair of ventral prolongations; anal cone not tubular (see Hungerford 1937, pl. II; habitus, Andersen 1982, fig. 438) *thomasi* Hungerford
- Male abdominal segment VIII modified, with an asymmetrical tumescence or tooth (Fig. 17); segments IX, X rotated at most 30° to 45°. Female without connexival spines or ventral prolongations; anal cone tubular (Figs. 23, 24) 3
- 3(2). Mesonotum of apterous forms without light markings, except golden or silvery setae forming stripes or spots. Male abdominal segment VIII broad, almost parallel sided, distally modified asymmetrically. Female abdominal segment VIII dorsally produced into long spine; ventrally anal cone long, curved, tubular (Figs. 23, 24) 4
- Mesonotum of apterous forms with median yellow longitudinal stripe (rarely completely dark). Male abdominal segment VIII narrow, tapering posteriorly, not expanded distally, with only a small tooth (see Drake and Harris 1934, pl. XXVI f, g). Female abdominal segment VIII dorsally triangular, ventrally with a short finger-like protuberance (anal cone) (see Matsuda 1960, fig. 471) .. *horvathi* Esaki
- 4(3). Vertex of head largely yellow, with a large elongate black region anteriorly, mostly anterad of eyes. Male abdominal segment VIII modified, with an asymmetrical tumescence (see Drake and Harris 1934, pl. XXV h). Female abdominal segment VIII dorsally with moderately long process (Fig. 23) *osborni* Drake and Harris
- Vertex of head largely black, with a small elongate yellow spot between eyes. Male abdominal segment VIII modified, with an asymmetrical lobe bearing two blunt teeth (see Drake and Harris 1934, pl. XXVI a). Female abdominal segment VIII dorsally with moderately long process (Fig. 24) *bidentatus* Champion
- 5(1). Male abdominal segment VIII modified, segments IX, X rotated a maximum of 45°. Female without connexival prolongations 6
- Male abdominal segment VIII modified, segments IX, X rotated about 90°. Female with large connexival prolongations 7
- 6(5). Male abdominal segment IX distally light; process of proctiger spatulate, usually hidden; segments IX, X rotated 5° to 10° (see Matsuda 1960, fig. 479). Female abdominal segment VIII dorsally triangular; ventrally with a triangular structure (see Matsuda 1960, fig. 472) .. *unidensatus* Champion
- Male abdominal segment IX distally dark; process of proctiger acuminate, exposed (Fig. 17); segments IX, X usually rotated 30° to 45°. Female abdominal segment VIII dorsally produced into long spine-like structure; ventrally with an asymmetrical spoon-shaped structure (Figs. 14, 15) .. *manzanaoae* n. sp.
- 7(5). Male abdominal segment VIII broad, short, slightly modified (Figs. 2, 5, 6). Female abdominal terminalia truncate (Figs. 1, 3, 4). *carvalhoi* n. sp.
- Male abdominal segment VIII longer, modified, with spinose or dentate lobes on right side (Figs. 10-12). Female abdominal segment VIII dorsally with short to long median digitate or spine-like prolongation (polymorphic, sometimes short), but never truncate (Figs. 7-9) 8
- 8(7). Distal lobe on right side of male abdominal segment VIII forming a single acute angle posteroventrally (Figs. 26, 27). Female abdominal segment VIII dorsally produced into a long posterodorsally directed spine (Fig. 25) *vivatus* Drake
- Distal lobe on right side of male abdominal segment VIII variably formed, but not forming a single acute angle posteroventrally. Female abdominal segment VIII dorsally with short or long process, but not posterodorsally directed 9
- 9(8). Distal lobe on right side of male abdominal segment VIII forming a posteriorly directed acute angle, plus a posteroventrally directed twisted spatulate lobe (see Polhemus and Polhemus 1983, fig. 1). Female abdominal segment VIII dorsally short, triangular; ventrally with a long process extending posteriorly far beyond

- tip of dorsal triangular plate on left side (see Hungerford 1937, pl. II)
 *woytkowskii* Hungerford
- Distal lobe on right side of male abdominal segment VIII variably formed, but not forming a single acute angle posteroventrally. Female abdominal segment VIII dorsally with short or long process; ventrally with short or long process, but not extending posteriorly far beyond dorsal structure 10
- 10(9). Distal lobe on right side of male abdominal segment VIII forming a posteriorly directed short spine, plus a posteroventrally directed acute angle (see Polhemus and Polhemus 1983, fig. 2). Female abdominal segment VIII dorsally produced into a long posteriorly directed finger-like process; ventrally with a long twisted process on left side extending posteriorly half the length of dorsal process (see Polhemus and Polhemus 1983, fig. 3)
 *spiculus* Polhemus & Polhemus
- Distal lobe on right side of male abdominal segment VIII variably formed, but not forming a short spine, plus an acute angle. Female abdominal segment VIII dorsally with short or long process; ventrally with short flap-like process not extending far posteriorly 11
- 11(10). Distal lobe on right side of male abdominal segment VIII forming a posteriorly directed twisted spatulate protuberance (see Hungerford 1937, pl. II). Female abdominal segment VIII dorsally triangular; ventrally with a short flap-like lobe on left side (see Matsuda 1960, fig. 460)
 *peruvianus* Hungerford
- Distal lobe on right side of male abdominal segment VIII forming two ventrally or posteroventrally directed spines. Female abdominal segment VIII dorsally with short or long process; ventrally with short flap-like process not extending far posteriorly 12
- 12(11). Distal lobe on right side of male abdominal segment VIII forming two posteroventrally directed teeth, ventral one longer; process of proctiger bifurcate distally (see Matsuda 1960, fig. 479). Female abdominal segment VIII dorsally with short stout process, directed posteroventrally; ventrally with short flap-like process covering left side of dorsal process (see Matsuda 1960, fig. 473) *variabilis* Hungerford
- Distal lobe on right side of male abdominal segment VIII forming two ventrally or posteroventrally directed spines of about equal length; process of proctiger not bifurcate distally. Female abdominal segment VIII dorsally with short or long process; ventrally with short flap-like process 13
- 13(12). Distal lobe on right side of male abdominal segment VIII forming two widely spaced posteroventrally directed stout spines (see Hungerford 1937, pl. II). Female abdominal segment VIII dorsally with short triangular process; ventrally with short flap-like process usually covering left side and part of right, almost hiding dorsal process (Figs. 28, 29)
 *williamsi* Hungerford
- Distal lobe on right side of male abdominal segment VIII forming two ventrally directed closely spaced spines of about equal length. Female abdominal segment VIII dorsally with short or long process; ventrally with short flap-like process 14
- 14(13). Distal lobe on right side of male abdominal segment VIII forming two ventrally directed stout spines with a pronounced rounded incision between (see Drake and Harris 1934, pl. XXVI c, d, e). Female abdominal segment VIII dorsally with short or long process, never bent ventrad; ventral short flap-like process with left lobe only developed (see Drake and Harris 1934, pl. XXVI b) *tridentatus* Esaki
- Distal lobe on right side of male abdominal segment VIII forming two ventrally directed stout spines with a shallow triangular incision between (Figs. 10-12). Female abdominal segment VIII dorsally with short or long process, often bent ventrad; ventral short flap-like process with both right and left lobes developed (Figs. 7-9) *anchicaya* n. sp.

POTAMOBATES SPECIES GROUPS AND SPECIES CHECKLIST

When this study began, we initially divided the genus *Potamobates* into species groups based on the complexity of the male and female abdominal terminalia, which exhibit the most salient species-specific characters in this genus. We then arranged these groups in what we considered to be rough phylogenetic order, with those exhib-

iting the largest number of plesiomorphic character states discussed first in the annotated checklist that follows. The geographic progression of phylogenetically increasing complexity from north to south suggested an ancestral stock in Mexico, and a secondary radiation southward through Mesoamerica into South America. The genus is currently known on this latter continent only in the Andean mountain chain from Colombia to Peru, and in the coastal sierras of northern Venezuela, inhabiting swift clear streams associated with mountainous terrain.

The checklist below, arranged by groups, contains all known species and includes the references for the original descriptions of all previously described species. Kirkaldy (1899) tentatively identified material from Ecuador as *P. bidentatus* and *P. unidentatus*; this material, in the Turin Museum, has not been restudied, but the identifications are almost certainly incorrect, and the records are not included here, because many new species have since been described from South America. New distributional records for described species are indicated with an asterisk (*).

P. thomasi group

Diagnosis.—Male genitalia simple, only slightly modified; segment IX not rotated; abdominal segment VIII not modified; proctiger with modest modification. Female with small connexival spines; abdominal segment VII ventrally modified, with two (1 + 1) lateral prolongations; VIII, IX not modified.

thomasi Hungerford 1937: 63. Mexico (western)

P. unidentatus group

Diagnosis.—Male genitalia relatively simple; segment IX slightly rotated, or rotated a maximum of 30° to 45°; abdominal segment VIII at most slightly modified ventrally. Female without significant connexival prolongations; abdominal segment VIII dorsally without or with modest median prolongation, ventrally without or with only

a modest prolongation; anal cone tubular, longest in Mexican species, shortest in *unidentatus*.

bidentatus Champion 1898: 155. Eastern Mexico (Catemaco area). [Note: *P. bidentatus*, collected by "Sallé, in Mexico" (1831–1834), remained an enigma ever since its original description, with the exact collection locality unknown, until Brailovsky and coworkers rediscovered it in the Sierra de Tuxtla, on a peninsula near Catemaco, where it is apparently endemic. The female, previously unknown, is figured herein (Fig. 24). *P. osborni* also occurs in the same general area, but further inland.]

horvathi Esaki 1926: 254. Belize, Colombia*, Costa Rica, Guatemala, Honduras, Mexico (Chiapas), Nicaragua*, Panama

manzanoae J. & D. Polhemus, n. sp. Colombia

osborni Drake & Harris 1928: 25. Eastern Mexico

unidentatus Champion 1898: 155. Colombia, Costa Rica, Panama

P. carvalhoi group

Diagnosis.—Male genitalia relatively simple, only slightly modified, very broad, short; segment IX rotated almost 90°; abdominal segment VIII slightly modified ventrally; proctiger modified, prolongation long, complex. Female tergite VII depressed, connexival prolongations long; ventrite VII prolonged, upturned distally; abdominal segments VIII, IX small, unmodified, symmetrical, withdrawn.

carvalhoi J. & D. Polhemus, n. sp. Colombia, Venezuela

P. tridentatus group

Diagnosis.—Male genitalia highly modified, segment IX strongly rotated; abdominal segment VIII modified, with spines or modest to large lobe-like extension on right side (sometimes divided); proctiger with a plate-like or long curved spine-like extension, distally always spine-like. Female with long connexival prolongations; abdominal

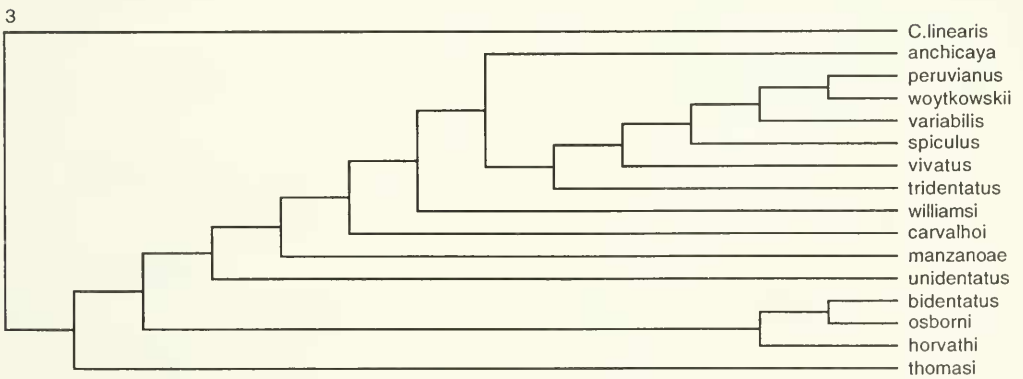
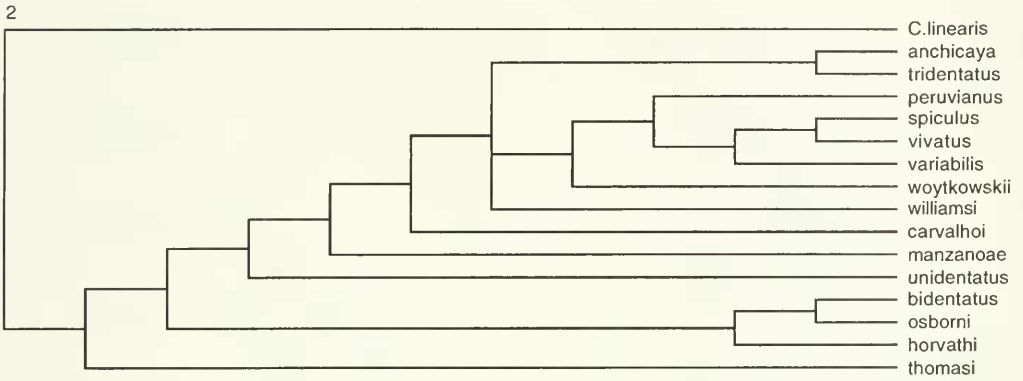
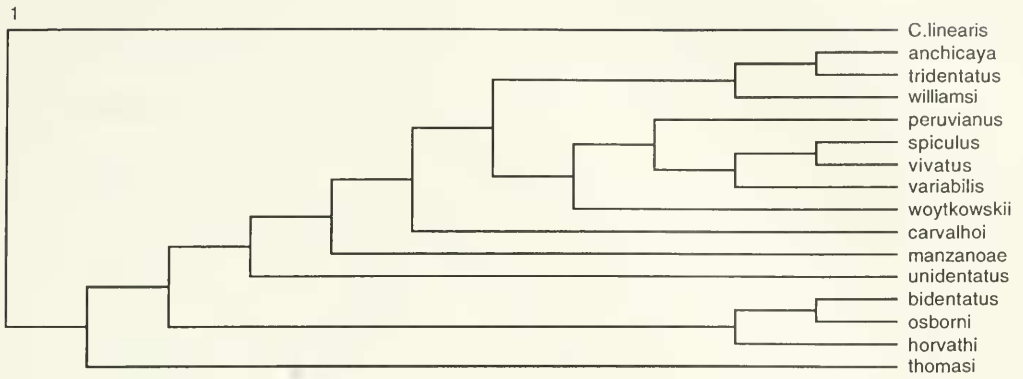


Fig. 30. Three most parsimonious trees generated from preliminary phylogenetic analysis of *Potamobates* species (see Appendices 1 and 2 for explanation).

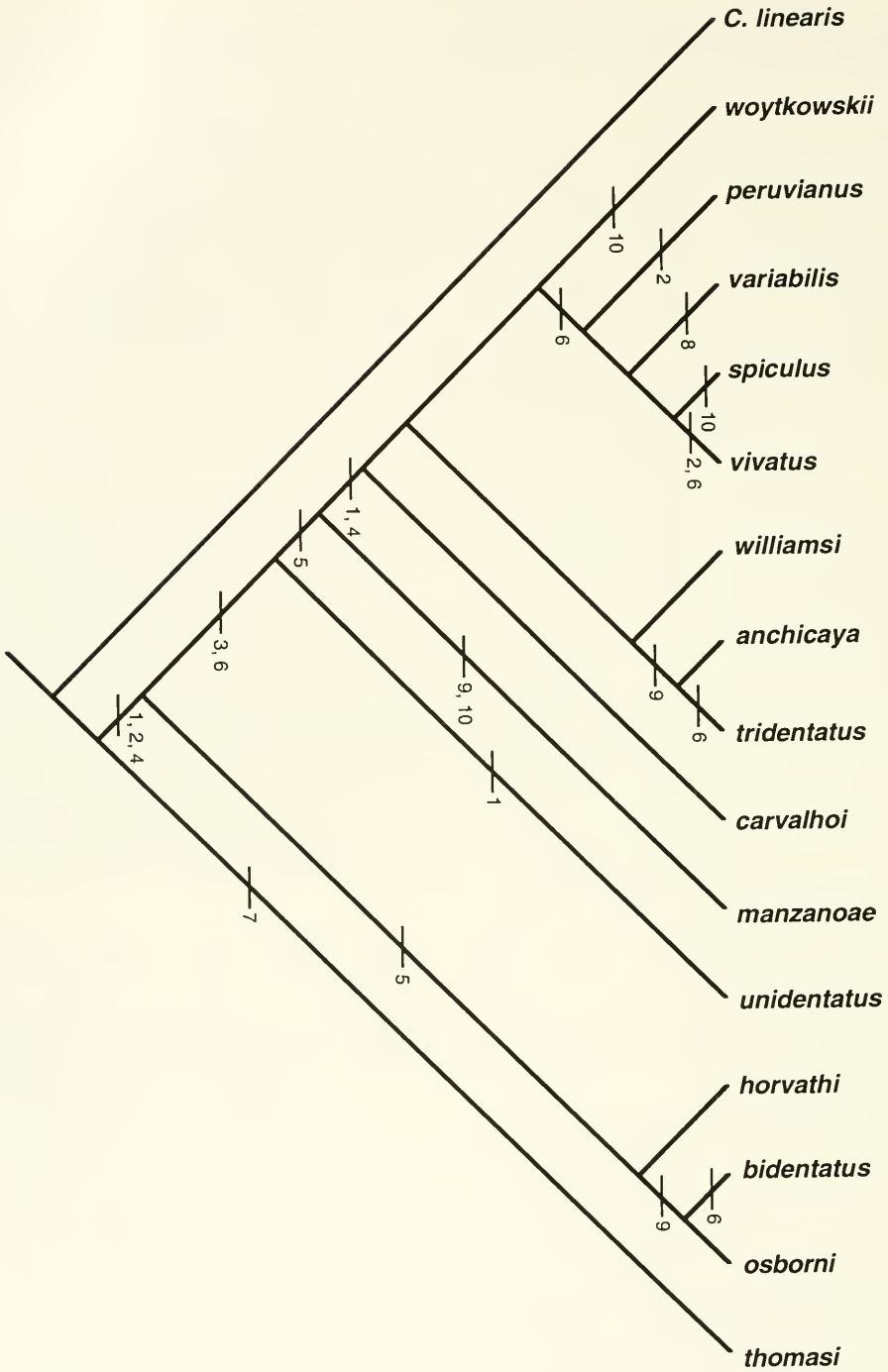


Fig. 31. Preferred cladogram for *Potamobates* species, with characters used in its construction (character numbering refers to that employed in Appendix 1). Numbers indicate characters changing from plesiomorphic to apomorphic state along a given branch.

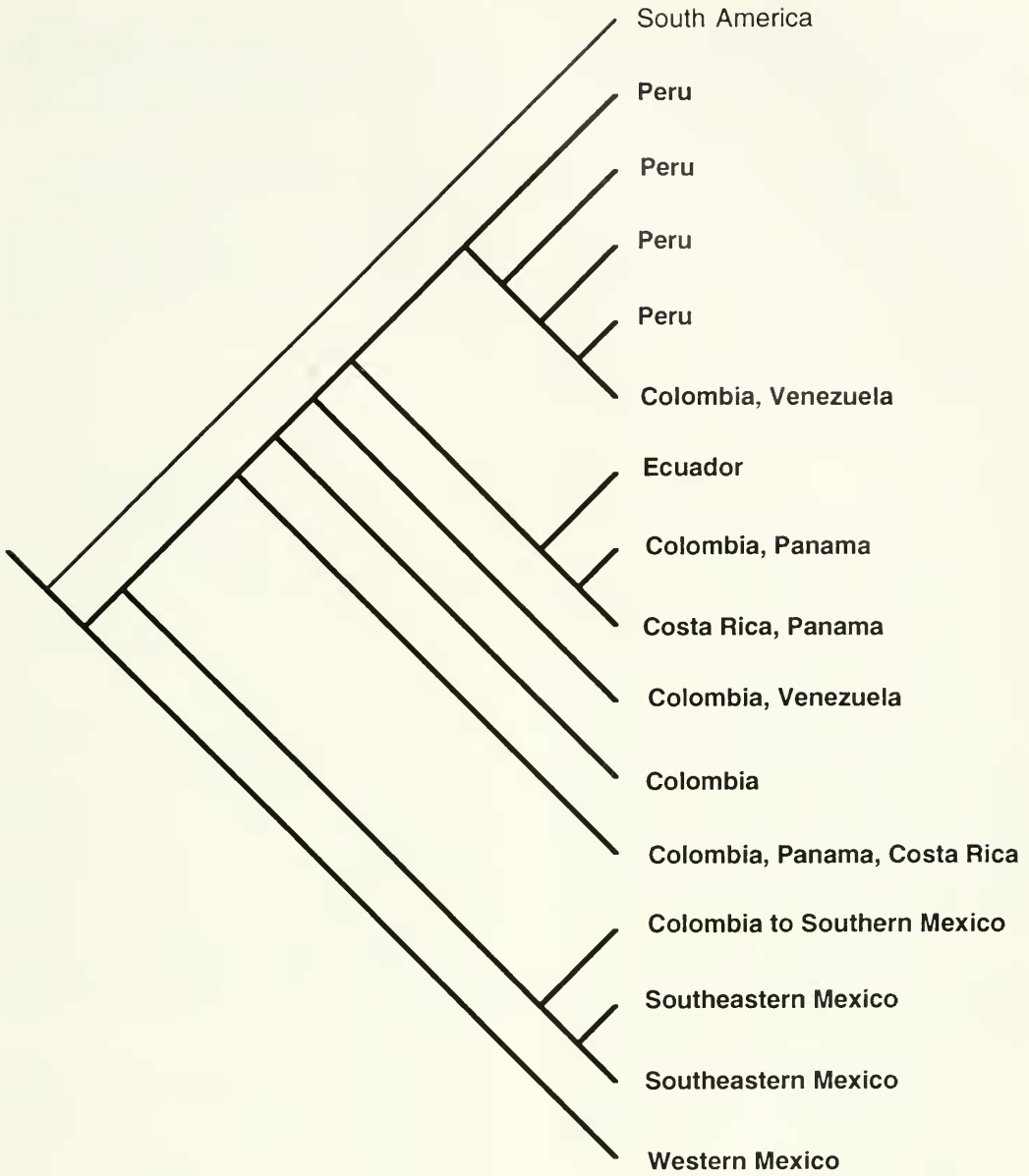


Fig. 32. Taxon-area cladogram based on preferred phylogeny for *Potamobates* species (see Fig. 31).

segment VIII modified, dorsally short, triangular or with a long median spine-like prolongation, ventrally with one or two short to long flap-like lobes, or with complex spoon-like prolongation.

anchicaya J. & D. Polhemus, n. sp. Colombia (western), Panama
peruvianus Hungerford 1936: 178. Peru

spiculus J. & D. Polhemus 1983: 286. Peru
tridentatus Esaki 1926: 251. Costa Rica, Panama
variabilis Hungerford 1938: 85. Peru
vivatus Drake & Roze 1954: 228. Colombia* (eastern), Venezuela
williamsi Hungerford 1932: 228. Ecuador
woytkowskii Hungerford 1937: 144. Peru

We have subsequently tested our hypothesis of species groupings via a preliminary cladistic analysis with a more comprehensive character set (see Appendices 1 and 2), which reveals that our groupings based on genitalic characters alone represent three monophyletic clades plus one basal paraphyletic grade (the *unidentatus* group). Our initial attempts to further discriminate two separate groupings among the South American species forming a clade at the far end of the tree (the *tridentatus* group) are not supported phylogenetically, since the entire suite of characters used contains systems that vary independently to such a degree that all groupings based on genitalic structures alone end up being polyphyletic in at least one of the most parsimonious trees.

The north to south biogeographic progression in genitalic character development alluded to previously was supported based on both our initial intuitive group hypothesis, and on the results of the phylogenetic analysis. In addition, the taxon-area cladogram derived from the phylogenetic analysis (Fig. 32) strikingly illustrates Colombia's pivotal role as a crossroads or Neotropical biogeography, which has acted as both a conduit between South America and Mesoamerica, and as an insular center of regional diversification. In marked contrast to the Peruvian *Potamobates* species, which all arise from a single clade, the Colombian *Potamobates* fauna contains members of all but one of the currently recognized intra-generic clades, including all the constituents of the paraphyletic *unidentatus* group as defined herein.

ACKNOWLEDGMENTS

We are indebted to the following colleagues for the loan or gift of material: M. R. Manzano, University de Valle de Cauca, Cali, Colombia (UVCC), and Nico Nieser, Tiel, The Netherlands (NNC). Holotypes of all new species described herein are deposited in the National Museum of Natural History, Smithsonian Institution, Washing-

ton, D.C. (USNM). All remaining material examined in the course of this study is held either in the foregoing institution, or in the J. T. Polhemus Collection, Englewood, Colorado (JTPEC). The field surveys that catalyzed this investigation were funded by National Geographic Society Grant 4092-89, and we gratefully acknowledge their continued support for research into the systematics and zoogeography of aquatic Heteroptera.

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- 30° to 45° max.; 3 = rotated approx. 90°.
2. Modifications to male first genital segment (abdominal segment VIII): 0 = not modified; 1 = distal ventral or lateral angle or angles; 2 = distal tumescence on left side; 3 = distal angulate lobe on left side; 4 = distal dentate lobe on left side.
 3. Median pronotal markings, male, female: 0 = roughly linear stripe; 1 = triangular or wedge shaped mark; 2 = absent.
 4. Female connexival spines: 0 = short spines, acuminate; 1 = absent; 2 = long, thickened.
 5. Female anal cone: 0 = not tubular; 1 = tubular, short; 2 = tubular, long.
 6. Mesonotum, medial markings: 0 = dark, no light marks; 1 = longitudinal light stripe; 2 = complex figures.
 7. Female ventrite VII: 0 = unmodified; 1 = modified, with prolongations.
 8. Modification of male proctiger: 0 = simple angle; 1 = long process, distally simple; 2 = long process, distally "dog head" shaped; 3 = long process, distally bifurcate; 4 = long process, distally strongly twisted (corkscrew fashion), at least 90°.
 9. Female first dorsal genital segment (tergite VIII): 0 = triangular; 1 = posterior extension digitate, short; 2 = posterior extension spinose, long.
 10. Female first ventral genital segment (ventrite VIII): 0 = triangular; 1 = truncate, hidden; 2 = short flaps, often asymmetrical; 3 = posterior extension spatulate, elongate, not twisted; 4 = posterior extension complex, twisted, narrow, spoon-shaped, long.

APPENDIX 1

Phylogenetic analysis of *Potamobates* species

Characters and polarity.—The set of characters listed below were employed in a preliminary analysis of *Potamobates* phylogeny. For each character, two or more discrete states were defined and symbolized by numbers. The most primitive (plesiomorphic) state was assigned a zero (0) value, and each successive derived (apomorphic) state a value of 1 or greater using successive integers. Multistate characters (those with more than two states) were ordered in linear transformation series, with 0 the most plesiomorphic state and each subsequent state assumed to be more apomorphic. Character polarities were generally determined *a priori* by complexity, with a 0 state being the least complex and therefore presumably the most plesiomorphic. In a few cases characters were also ordered by comparison with the outgroup (*Cylindrostethus linearis*).

1. Male distal genital segments (abdominal segments IX, X): 0 = not rotated; 1 = rotated 5° to 10° max.; 2 = rotated

Computer analysis.—A cladistic analysis of *Potamobates* species was performed using the program PAUP 3.0.m (D. L. Swofford, Illinois Natural History Survey). This program generates phylogenies using the principle of maximum parsimony, and eliminates trees that are identical due to

zero length branches. The ingroup taxa for the analysis were the 15 species in the genus *Potamobates*, while the outgroup for the analysis was *Cylindrostethus linearis*, another Neotropical member of the subfamily Cylindrostethinae. Using the rooting option on PAUP, the outgroup was constrained to be a monophyletic sister group to the ingroup.

The PAUP analysis was carried out using the *branch and bound* option, using the furthest addition sequence and collapsing zero length branches to yield polytomies. This analysis produced three most parsimonious trees, depicted in Fig. 30. These trees had lengths of 47, consistency indices of 0.53, and retention indices of 0.52. Two of the three trees were fully resolved, while one of the trees (tree 2 of Fig. 30) had an internal polytomy at the base of the clade containing the insular South American species. Based on evolutionary considerations involving genitalic characters and biogeographic parsimony, one of the two fully resolved trees (tree 1 of Fig. 30) was chosen as a preferred phylogeny, and is shown (with some branches swapped) in Fig. 31. A taxon-area cladogram based on this tree is given in Fig.

32, and depicts a clear biogeographic progression from plesiomorphic clades occupying Mesoamerica to apomorphic clades in South America.

APPENDIX 2. Coding of characters for phylogenetic analysis. Character matrix for *Potamobates* species (character states are ordered sequentially for characters 1–10 as given in Appendix 1).

Taxon	Character States
<i>Cylindrostethus linearis</i> ¹	0000100001
<i>Potamobates anchicaya</i>	3412020122
<i>Potamobates bidentatus</i>	2101200221
<i>Potamobates carvalhoi</i>	3212020201
<i>Potamobates horvathi</i>	2101210000
<i>Potamobates manzanoae</i>	2111020024
<i>Potamobates osborni</i>	2101210121
<i>Potamobates peruvianus</i>	3312000402
<i>Potamobates spiculus</i>	3412000423
<i>Potamobates thomasi</i>	0000111000
<i>Potamobates tridentatus</i>	3412010122
<i>Potamobates unidentatus</i>	1111120002
<i>Potamobates variabilis</i>	3412000312
<i>Potamobates vivatus</i>	3312010422
<i>Potamobates williamsi</i>	3412020102
<i>Potamobates woytkowskii</i>	3412020403

¹ Outgroup.